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Birch and conifer deadwood favour early establishment and shade tolerance in yellow birch juveniles growing in sugar maple dominated stands

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ABSTRACT

Small-seeded tree species such as Yellow birch (YB: *Betula alleghaniensis* Britt.) require deadwood or mineral soil for their establishment. Although much research has been done comparing YB germination on leaf litter vs. exposed mineral soil, less is known about deadwood as a seedbed and how different seedbeds affect YB early growth along light availability and size gradients. We examine how three common seedbeds (deadwood, moss cover on deadwood, and mineral soil) affected establishment and growth, biomass partitioning and morphological traits of YB juveniles growing in the understory of temperate mixed deciduous and coniferous forests in Southern Quebec. A total of 274 YB were sampled in four sugar maple dominated northern hardwoods where selective-cuts had been applied 6 and 15 years prior to sampling. Over 75% of the YB found on deadwood were on material of birch and conifer origin, although these species made less than 40% of the basal area. YB juveniles growing on deadwood showed traits that improve survival in shade, such as reduced height growth for tall plants, higher efficiency in resource capture, and multi-layered crowns. Our results demonstrate the importance of deadwood of birch and conifer origin in maintaining an abundant, natural, spatially well-distributed, and multi-storied regeneration of YB.

Keywords: *Betula alleghaniensis*, seedbed, deadwood, biomass partitioning, selective-cut.

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INTRODUCTION

Substrate has a strong potential effect on micro-environmental factors (e.g., water and nutrient availability) that can in turn influence the performance and morphology of tree juveniles (Sanchez-Gomez *et al.*, 2006; Portsmuth and Niinemets, 2007). However, how the responses in traits and morphology of one tree species (intraspecific level) would vary as a function of contrasting seedbeds has received much less attention compared to light-induced (Beaudet and Messier, 1998; Paquette *et al.*, 2007; Ameztegui and Coll, 2011), or ontogenetic (Delagrange *et al.*, 2004; Lusk, 2007) variations. The general assumption is that individuals of a given species and equivalent size will perform more or less alike under similar light conditions, despite the fact that individuals in close proximity may occupy highly contrasting substrates. Therefore, there is a need to better understand the performance and the mechanistic responses of species on various seedbeds along size and light gradients.

In the north-eastern hardwoods of North America, substrate availability is one of the main factors limiting seedling establishment, particularly for small-seeded species such as yellow birch (YB; *Betula alleghaniensis* Britt.) (Gray and Spies, 1997; Caspersen and Saprunoff, 2005). Small seeds benefit from a direct contact with a high-porosity substrate, and exposed mineral soil and decomposed deadwood often provide adequate growing conditions compared to those that prevail on the forest floor (Harmon *et al.*, 1986; Gray and Spies, 1997; Cornett *et al.*, 2000; Simard *et al.*, 2003). Several studies have assessed the effects of seedbed on YB establishment, growth and juvenile survivorship (i.e. Godman and Krefting, 1960, Gastaldello *et al*. 2007, Shield *et al.* 2007, Lorenzetti *et al.*, 2008), but most of them have focused on the differences between leaf litter and mineral soil, and only a few have assessed the effects of decaying wood

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on YB performance and survivorship (Marx and Walters, 2006; 2008). Moreover, some intrinsic physical properties of deadwood, such as the species identity of wood pieces (Marx and Walters, 2008; Bolton and D'Amato, 2011) and the decay class of deadwood (Ran *et al.*, 2010), can affect seedling demography, but their effect on life-history traits are largely unknown for many tree species.

Here, we present a study that quantifies YB recruitment, performance and morphology as a function of light availability, juvenile size and seedbed type in sugar maple dominated forests of southern Quebec (Canada). YB is a valuable, shade midtolerant species reputed to regenerate preferentially on litter-free substrates and deadwood (Houle, 1998; Barras and Kellman, 2002), whose relative abundance has greatly diminished in stands managed by single-tree selective cutting (Poznanovic *et al.,* 2014). Its low recruitment has been attributed to insufficient gap size (Webster and Jensen, 2007), browsing by white-tailed deer (Kern *et al.*, 2012) or the paucity of adequate seedbeds for seedling establishment in managed stands (Bolton and D'Amato, 2011), and group selection cuttings have been suggested as a means of promoting its regeneration in managed stands (Poznanovic *et al.,* 2014).

The first objective of this study was to compare establishment patterns of YB juveniles between the main seedbed types known to be important for YB (mainly deadwood and mineral soil). In relation with this first objective, we investigated the following questions: (*i*) Does the relative abundance of YB vary spatially as a function of seedbed type? (*ii*) How do the age and size distributions of YB individuals vary as a function of seedbeds? (*iii*) Does the deadwood species identity and decay class affect its capacity to give shelter to YB seedlings?

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The second objective was to examine the variation in growth, biomass partitioning, root architecture, and other morphological traits of YB seedlings and saplings in relation to light availability, tree size, and seedbed type. Our main hypothesis is that the various traits that are important for YB growth and survival would differ in their expression between decaying wood and mineral soil, and that this could influence YB's ability to tolerate shade. We expected, for equal light conditions and tree size, seedlings established on deadwood would have lower height growth and a greater allocation to roots as compared to seedlings established on MS.

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MATERIALS AND METHODS

Study sites and stand selection

The study was conducted from early May through mid-September 2010 in the Réserve faunique Papineau-Labelle, located in south-western Quebec, Canada (46°1'N, 75°19'W). The forest in this region is part of the sugar maple (*Acer saccharum* Marsh.) – yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domain of the temperate mixed deciduous and coniferous forests of north-eastern North America. Mean annual rainfall in the study area is around 1000 mm, with 25% falling as snow. Mean annual daily temperature ranges from 2.5 to 5°C and growing season length varies from 163 to 182 days. Surface deposits in the region are thin glacial tills where bedrock outcrops are sporadic. Soils are well- to moderately well-drained and range from eluviated dystric brunisols to humo-ferric podzols. Humus mainly consists of moder and mor types, depending on the location and the associated tree species.

We selected four forest stands in the area that had been recently harvested by selective cutting (SC) and in which stand basal area was approximately 20 m^2 ha^{-1} after treatment. Two of the stands were cut in 2004 (recent cut) and the other two were cut either in 1994 or 1995 (old cut), ensuring a broad gradient of regeneration size. All stands had been harvested in accordance with provincial guidelines prescribed for SC treatment (Bédard and Majcen, 2003). The forest overstory of the sampled stands was representative of the domain type, and sugar maple and yellow birch (YB) were the dominant tree species in the canopy of the four stands. Several other tree species were present in mixture in lower proportions, including balsam fir (*Abies balsamea* (L.) Miller), red maple (*Acer rubrum* L.), eastern white-cedar (*Thuja occidentalis* L.), American basswood (*Tilia americana* L.), or American beech (*Fagus grandifolia* Ehrh.).

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1

2 **Seedling abundance and establishment patterns**

3 We used the line-transect method (grid) to evaluate YB abundance in the understory. A total of
4 36 transects were positioned in the studied stands. Transect lines were oriented north-south and
5 separated from one another by 50 m. Depending on stand size and shape, transect length and
6 number varied from 50 to 500 m and from 4 to 12, respectively. Along each transect, every
7 occurrence of YB regeneration (ranging from 15 to 330 cm in height) was recorded within 5
8 metres on either side of the transect line. We did not include seedlings of less than 15 cm in
9 height to avoid first year seedlings. We recorded the height (along the main stem), the seedbed
10 and the microsite type for each of the 1015 identified YB, and an estimation of canopy opening
11 was obtained using a spherical densiometer. Seedbed referred to the nature of the substrate, and
12 was identified visually as either mineral soil (MS), mosses (M), deadwood (DW), moss cover on
13 deadwood (MDW), or humus (H). The microsite type referred to the fine-scale ground
14 heterogeneity where the individuals were established and included pits and mounds (PM), skid
15 trails (ST), stumps (S), trunks (T), and wood debris (WD). An "unknown" category was assigned
16 when a clear determination was not possible. For every juvenile occurrence on deadwood
17 (classes DW and MDW), we identified the decay stage from 1 to 5 following Angers *et al*.,
18 (2005) and determined the identity of the species from which the deadwood was derived. When
19 possible, the species was determined in the field using the presence of bark covering the bole as
20 criterion for identification. Otherwise, small samples of less-decomposed sections were collected
21 for later species identification following protocol provided by Marx and Walters (2008). Every

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YB individual was identified in the field by a unique number for further measurements, and its location was recorded.

Tree measurements and harvesting

We performed a destructive sampling on a semi-random subsample from the entire population of juveniles marked along the transects. From early August to mid-September 2010, 274 individuals with no signs of browsing were selected so that a large gradient of size and light conditions was represented within each stand. Approximately the same number of individuals were chosen from each of the main recorded seedbed types: DW (n = 85); MDW (n = 96); and MS (n = 93). Other seedbed types (humus and mosses) were discarded, since we observed very few YB juveniles growing on them along the transects. For each individual in the subsample, we determined trunk size and total number of live branches (see Delagrange *et al*., 2004). We measured height increment for the year 2010 by measuring the distance from the shoot apex to the bud scales of the penultimate year's shoot, and we calculated averaged annual height growth (AHG, $cm \cdot year^{-1}$) by dividing total height by age. The age of each individual was determined at the base of the stem under a dissecting microscope. We also took hemispherical canopy photographs to determine the amount of light reaching the top of each individual included in the subsample. Photographs were taken on overcast days, and were analyzed using Gap Light Analyzer (GLA v.2.0). At each of these locations we estimated basal area of each tree species using a prism, and basal area values were averaged by stand.

After measurements, plants were dissected to determine biomass allocation and a set of traits. The fresh materials were separated into roots, stem, branches, and leaves, and the three latter

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portions were weighted after being oven-dried at 65°C for 48 h. Roots were washed free of mineral soil and deadwood after drying, and dried again before weighting. We used a 32-mesh sieve during washing to avoid loss of fine roots. Entire dry root systems of all individuals were separated in different diameter classes (fine, $\leqslant$ 1 mm; medium, 1.01 mm - 2mm; coarse, > 2 mm), which were evaluated using a digital caliper.

Biomass partitioning and leaf and root morphology

We summed all biomass components to obtain total tree dry mass (DM) and calculated the percentage of all plant components in total tree DM (branch, stem, leaf and total root) and the ratio of photosynthetic (PT) to non-photosynthetic tissue (NPT). We also calculated the fine root mass ratio (FRMR, fine root to total tree dry mass) and the root:shoot ratio (RSR; using total root mass). We determined root morphology from a subsample of the total root material extracted for each plant. At least three root sections of less than 0.5 mm diameter (sub-subsamples) were selected for each individual, and we scanned the root sections at a resolution of 500 dpi and used WinRhizo (Regent Instruments Inc., Québec City, Québec, Canada) to determine root length. The specific root length (SRL, $m \cdot g^{-1}$) was then determined as the length/biomass ratio.

At the moment of plant extraction, a subsample of leaves was collected (at least 25 leaves per tree), and the leaf area was measured using LI-3100 area meter (Licor Inc., Lincoln, NE, USA) within the day of leaf harvesting. Subsamples were then dried and weighed separately from the total leaf samples, and we calculated the leaf area ratio (subsample leaf area · subsample leaf dry $mass^{-1}$). This variable was then multiplied by total plant leaf dry mass to obtain total leaf area

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(cm^2). We also calculated leaf area ratio (LAR; m^2 g^{-1} plant) of total plant dry mass and leaf area as a ratio of aerial plant dry mass (aerial LAR; m^2 g^{-1} plant).

Data analyses

We compared the frequency distributions of YB seedling occurrences among seedbed and microsite types in old vs. recent selection cuts through a chi-square test. The differences in the quantitative explanatory variables (light conditions, tree height, and age) across seedbed types were assessed through a one-way ANOVA, and post-hoc Tukey–Kramer HSD tests revealed which seedbeds were significantly different from one another. Differences in the explanatory variables between old and recent cut stands were assessed using a t-test.

To determine the effect of seedbed on the morphological traits and growth patterns (dependent variables) we used a mixed-model analysis of covariance (ANCOVA), using restricted maximum likelihood (REML) to estimate parameters in the model. Predictors were seedbed, light availability (canopy openness), plant size (total height), and their interactions. To insure that mean differences were attributable to the effect of seedbed type (fixed main effect), we treated light availability and plant size as covariates, whereas site was treated as a random effect. In some cases, dependent variables were transformed (log- or square-root) to meet assumptions of homoscedasticity and normality. We verified the assumption of homogeneity of slopes by determining the significance of the interaction terms between seedbed and the covariates. When the interaction between factor (seedbed) and covariates (size and/or canopy openness) were significant, interpretations were made only on the interactions and not on the main effects.

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Finally, the response of growth, biomass distribution and morphological variables to variation in plant height was investigated for each seedbed type using linear regression on model's predicted values. This was done only for parameters where interaction between size and seedbed was found to be significant. All analyses were conducted using JMP 9.0 (SAS Institute Inc., Cary, NC).

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RESULTS

Occurrences of YB juveniles across seedbed types and microsites

The frequency distributions of YB juveniles across different types of seedbeds and microsites revealed significant differences between old and recent SC (Seedbed: $\chi^2 = 36.87$, $df = 2$, $p < 0.0001$; Microsite: $\chi^2 = 81.58$, $df = 5$, $p < 0.0001$). Overall, YB juveniles were found mainly on MDW (46% and 29% of the total abundance in old and recent SC, respectively), followed by MS (34% and 41%), whereas they were less frequent on DW (around 20% in both types of SC) and virtually absent from other seedbed types, including mosses or humus (Fig. 1A). The proportion of YB juveniles growing on MS was slightly higher at recently harvested stands, whereas the trend was the opposite for MDW. With regard to microsites, YB juveniles mostly appeared in skid trails (ST), trunks (T) and stumps (S), but the frequency on the latter was significantly higher in old SC than in recently harvested stands (Fig 1B). Occurrences on mineral soil were mostly restricted to skid trails (83%) and, to a lesser extent, to pits and mounds (PM, 15%), whereas YB juveniles growing on deadwood were found in similar proportions on trunks and stumps and, to a lesser extent, in woody debris (data not shown).

Effect of seedbed on age and size distributions of YB juveniles

The age range of juvenile YB across all stands spanned three decades, from 2 to 33 years. Overall, YB juveniles growing in recent SC were younger and shorter than those growing in old SC, and received more light (Table 1). The average YB juvenile in old SC – in which selective cutting had been applied 15 years before sampling – was 12.6 years old and 137.9 cm height. In contrast, average juvenile in recent SC stands – where SC had been applied only 6 years before

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sampling – was 9.0 years old. There were no differences in height or light availability across seedbeds, but there was a significant interaction beween seedbed type and time since cutting in seedling age. In recent SC, those juveniles growing in deadwood (DW or MDW) were 2 to 2.5 years older than those growing in mineral soil (Table 1).

Effect of deadwood species and decay class on YB juvenile abundance

The distribution of juveniles across deadwood species was different from their relative abundance in the forest overstory ($\chi^2 = 1117.5$, $df = 4$, $p < 0.0001$). Most of the YB juveniles growing on deadwood were found on conifer logs (>60%), despite conifers only represented 20% of the total current basal area (Fig. 2). On the other hand, even though sugar maple was the dominant species in the study forests and accounted for more than 50% of the total basal area, less than 10% of the YB juveniles growing on deadwood were found on this species. The proportion of YB juveniles in YB deadwood was slightly higher than would be expected based on its relative abundance in the forest, whereas very few seedlings were found growing in other deciduous species (Fig. 2). Most YB juveniles on deadwood were found in well-decomposed deadwood, notably decay classes 4 (little to no bark remain, broken bole) or 5 (coarse woody debris). We noted that in recent SC there was a significantly higher proportion of YB juveniles in decay class 2 (bark loose, wood still hard) and lower in class 4, as compared to old SC (Fig. 3).

Effect of seedbed, canopy opening and individual size on performance and morphology

Absolute height growth in 2010 (AG) and averaged height growth (AHG) were both strongly influenced by tree height and canopy opening (see Growth section in Table 2). There was a

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significant interaction between seedbed type and tree height for both growth variables: individuals established on MS increased their growth faster with tree size, whereas individuals on deadwood had a much lower growth rate along the size gradient, and their growth rate was lower for heights above 100 cm (Fig. 4).

The entire set of variables related to biomass partitioning were strongly affected by tree size, except for the percentage of biomass allocated to roots and the root: shoot ratio. The biomass percentages apportioned to stems and branches increased with size, whereas all other parameters decreased (Table 2). There was also a marginally significant effect of light availability on the allocation to leaves and the ratio of photosynthetic to non-photosynthetic tissues (TP/TNP), whereas seedbed only affected significantly the fine root mass ratio (FRMR) and aerial LAR. Individuals on DW and MDW had a significantly higher FRMR than individuals established on MS (Figure 5a). Similarly, aerial LAR was higher on MDW than on DW or MS (Figure 5b). We also detected a significant interaction between tree size and seedbed for branch allocation (% Branch) and for absolute number of live branches, indicating that biomass allocated to branches along the size gradient varies between seedbeds.

DISCUSSION

Patterns of YB establishment in relation to seedbeds and microsites

The much greater proportion of YB found on deadwood as compared to other seedbeds contribute to the growing body of studies demonstrating its importance for both the establishment and subsequent survival of this tree species (McGee, 2001; Marx and Walters, 2006; 2008). Previous studies in similar forests estimate that deadwood occupies between 2.5%

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to 5% of the total ground surface area (McGee and Birmingham, 1997; Beaudet *et al.*, 2014), but we observed that the proportion of YB juveniles growing on this seedbed was much higher (>50%). The presence of YB juveniles on MS, although substantial (35%) was not much different from estimates of the total projected area of forest ground surface occupied by MS in stands managed by SC, which usually ranges between 15 and 35% (Lorenzetti *et al.*, 2008; Malo and Messier, 2011; Beaudet *et al.*, 2014).

We found a great proportion of YB juveniles on deadwood of YB and conifer species, much higher than would be expected based on their relative presence in the overstory, whereas very few YB juveniles were present on maple deadwood. These results agree with previous findings reporting a low presence of YB on maple deadwood (Marx and Walters, 2006; 2008), and a greater representativeness of YB saplings and seedlings on large pieces of coniferous coarse woody debris compared to deciduous species (Bolton and D'Amato, 2011). The exact mechanisms that could be implicated in the preference of YB for deadwood of coniferous species remain unclear, but the observed slower decay rate of many conifer wood species as compared to deciduous species (Harmon *et al.*, 1986; Tyrrell and Crow, 1994) might play an important role. In this regard, YB bark is highly resistant to disintegration and thus its deadwood exhibits a low decay rate compared to other hardwoods such as sugar maple (Arthur *et al.*, 1993; Marx, 2005), which seems to further confirm the importance of decay rate. A slower decay rate can provide YB juveniles the chance to develop a larger root system anchored in the underlying MS before the collapse of the wood substrate. Moreover, well-decomposed deadwood provides an easier substrate for roots to penetrate and anchor (Narukawa and Yamamoto, 2003), with higher water-holding capacity (Cornett *et al.*, 2000), reduced competition (Harmon and Franklin, 1989;

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Coomes *et al.*, 2005), and the presence of beneficial decomposer fungi (Fukasawa, 2012). A slower decay rate also allows for a greater presence of mosses on deadwood, which can facilitate seedling establishment through greater seed retention (Harmon, 1989) and an amelioration of moisture conditions of the humus-layer immediately beneath the moss (Nakamura, 1992; Parent *et al.*, 2003). Nevertheless, other species-specific characteristics of deadwood such as nutrient availability (Marx and Walters, 2006), differences in mycorrhizal inoculation or fungal decay type (Marx, 2005), are all plausible factors that may have contributed to the higher juvenile abundance and survival of YB juveniles on conifer and birch deadwood.

YB recruitment in unmanaged forests has generally been associated to disturbance events increasing the proportion of disturbed forest floor, after which this species can profit its capacity to rapidly germinate when in favourable conditions (Webster and Jensen, 2007; Gasser *et al.*, 2010). Therefore, it was concluded that YB had a limited capacity for maintaining a bank of suppressed individuals in the understory, and some studies reporting an abundant presence of advanced regeneration prior to the harvest were generally considered as exceptions and not the rule (Stearns, 1951; White *et al.*, 1985; Webster and Lorimer, 2005). Here, we found that regeneration cohorts did not follow the same temporal pattern of establishment on different seedbed types, and advanced regeneration (i.e. YB juveniles established prior to harvesting) were more numerous on deadwood (both DW and MDW) than on MS, as previously suggested by Bolton and D'Amato (2011). Moreover, we found that YB has the potential to establish almost continuously if adequate seedbeds (especially deadwood) are available, and can persist for more than 20 years in the understory as seedlings or saplings. Therefore, we argue that the occurrence

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of YB advanced regeneration is not as anecdotal as previously reported, even in the absence of major canopy disturbances over long periods, but largely depends on the availability of suitable seedbeds.

Performance, morphology and biomass partitioning of YB juveniles as a function of seedbed type

Overall, our results showed that measured traits were greatly influenced by tree size and light, and to a less extent by seedbed. Ontogenetic effects– i.e., the effect of developmental stage or size of the plant – are known to have a very strong effect on most allocation ratios, morphology and growth (Messier and Nikinmaa, 2000; Delagrange *et al.*, 2004; Niinemets, 2006), whereas we only detected a significant effect of light for traits that were related to leaf (allocation and morphology) and growth, but with no interaction effect of light with seedbed. Contrary to our expectations, seedbed type had no direct effect on juvenile height growth, but there was a significant interaction between this factor and the size of the individuals for both growth parameters. YB juveniles growing on DW or MDW had lower height growth rate than those growing on MS when they reached a height around 100 cm or taller. The ability to reduce height growth and to avoid reaching a 'critical height' has been related to greater survival in low-light environments for several species, since it allows them to avoid the increased respiration and maintenance costs associated with larger sizes (Messier *et al.*, 1999; Kneeshaw et al., 2006, Ameztegui and Coll 2011). We also observed that YB juveniles were more efficient in resource capture when growing on deadwood (they had both higher aerial LAR and FRMR), which would also favour carbon gain on light-limited environments (Walters and Reich, 1999; Portsmuth and

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Niinemets, 2007). Finally, the higher number of living branches found on YB juveniles growing on deadwood indicates a multi-layered crown that favours light interception in low-light environments. Our results thus indicate that YB juveniles growing on deadwood may show enhanced capacity for survival in shade, thereby increasing their capacity to survive as advance regeneration in light-limited environments, as we observed.

Implications for forest management

Regeneration of YB in managed stands has frequently been said to be favoured by skidding machinery traffic, which considerably disturb forest floor and increase the availability of mineral soil as compared to unmanaged stands, where it rarely exceeds 1% (Beaudet *et al.* 2014). Indeed, we found 35% of the YB juveniles to be on MS, and they were located almost exclusively on skid trails. However, an excessive dependence on skid trails for regeneration of YB can have some risks. Beaudet *et al.* (2014) have recently shown that the increase in the availability of MS associated to skid trails is only noticeable during the first years after the harvest, after which the MS is covered by leaf litter. Thus, the successful recruitment of YB seedlings would be at risk if there is no mast year in the 2-3 years following a harvest. Even though, the same skid trails are often used in every harvest period (every 20-30 years for SC; McGee and Birmingham, 1997), so the cohort that was established on the trails after the previous harvest risks of being damaged by the reutilization of old skid trails. A careful planning and design of the skid trails abundance and layout would thus be required in order to ensure the establishment of YB regeneration on skid trails and its preservation.

Without these considerations, YB recruitment on managed stands is likely to largely depend on the availability of suitable species and sizes of deadwood. Deadwood availability is more stable

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over time than MS, and it is thus important to ensure the long-term regeneration of small-seeded species such as YB. Yet, there has been a long-lasting lack of consideration for the need of deadwood retention in managed stands, and reduction in coarse woody debris volume and size in stands managed through selective cuttings have already been reported in different studies (McGee and Birmingham, 1997; Angers *et al.*, 2005; Beaudet et al. 2014), leading to a decline of the abundance of YB in managed stands. Moreover, and given the importance of the specific identity of deadwood that we observed in this study, the depletion of coniferous tree species that has been reported in many managed stands across north-eastern North America (Burton *et al.*, 2009; Dupuis *et al.*, 2011) is likely to have also contributed to the decline of YB in the past. Therefore, specific guidelines and management plans should incorporate the need to increase the retention of deadwood of species suitable to act as nurse logs for YB. If these efforts are not implemented, potential long-term impacts on YB regeneration on managed stands can be expected, which may lead to effects on the future composition of some forest types (Harmon and Franklin, 1989; Caspersen and Saprunoff, 2005; Marx and Walters, 2008).

Conclusion

The results of our study underscore the important role that deadwood plays, particularly of conifer and birch origin, in providing an adequate seedbed for establishment and survival of yellow birch in sugar maple stands, as has been suggested in previous studies. Our study also highlighted establishment limitations for the cohorts of individuals that were found on mineral soil and which were mainly restricted to skid trails. Thus, the spatial distribution of YB can be restricted within stands that lack the appropriate deadwood seedbed and that are managed by

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partial cuts. Seedbed had a relatively limited, but direct and significant effect in explaining some trait variation compared to strong ontogenetic effects. However, the lower growth rate that was reported for individuals that had attained a height of about 100 cm on deadwood dramatically influenced traits linked with ontogenetic effects. This slowed growth coupled with a multi-layered crown and higher values of FRMR and LAR could increase the survival capacity of YB in the understory. We suggest that these intra-specific responses favour the capacity for creating and maintaining a bank of suppressed individuals as advanced regeneration. The natural regeneration processes of this species have to be reconsidered under these conditions and partial cutting practices should be implemented to maintain an adequate level of large woody debris of yellow birch and conifer origin.

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TABLES

Table 1 Tree height, age and amount of light reaching the top of each individual for yellow birch juveniles harvested at different seedbeds at four temperate forests where selective-cuts (SC) had been applied (6 or 15 years prior to sampling).

	N	Tree height (cm)	Age (years)	Crown Openness (%)
Old SC (1994-95)				
Mineral soil	42	137.17 ± 10.57 a	12.88 ± 0.62 a	21.24 ± 0.91 a
Deadwood	42	139.19 ± 8.63 a	12.88 ± 0.57 a	20.71 ± 1.02 a
Mosses on deadwood	62	137.24 ± 9.58 a	12.05 ± 0.62 a	20.76 ± 0.86 a
Recent SC (2004)				
Mineral soil	43	118.27 ± 9.94 a	7.56 ± 0.44 b	25.72 ±1.46 a
Deadwood	51	121.70 ± 9.36 a	9.84 ± 0.73 a	23.55 ±1.12 a
Mosses on deadwood	35	103.87 ± 9.92 a	9.53 ± 0.82 a	24.07 ±1.03 a

Values are means ± 1 SE. Means followed by the same letter do not differ significantly at the $P < 0.05$ threshold (Tukey–Kramer HSD).

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Table 2: Summary of ANCOVA *P*-values for relationships between growth, allocation, leaf performance and morphological root parameters, with canopy opening (CO; %) and total height (TS; cm) as covariates, seedbed (SD) as a fixed factor and site as a random factor.

	Canopy opening (CO)	Tree Size (TS)	Seedbed (SD)	CO x SD	TS x SD	R^2
Growth						
AG	0.0005	**<0.0001**	0.6701	0.7616	**0.0233**	0.35
AHG	0.2513	**<0.0001**	0.5739	0.5672	**0.0087**	0.64
Allocation						
% Branch	0.8847	**<0.0001**	0.0532	0.9948	**0.0065**	0.36
% Stem	0.3043	**<0.0001**	0.1016	0.8677	0.8992	0.27
% Leaf	**0.0480**	**<0.0001**	0.1367	0.3346	0.5186	0.62
% Root	0.8501	0.8108	0.1430	0.5895	0.3164	0.23
PT/NPT	0.0562	**<0.0001**	0.0794	0.3466	0.3467	0.62
FRMR	0.2137	**<0.0001**	**<0.0001**	0.8443	0.1984	0.50
Root/Shoot	0.9135	0.6647	0.1299	0.6025	0.3340	0.23
Morphology						
Nb. Branches	0.8005	**<0.0001**	0.8169	0.9468	**0.0219**	0.32
LMA	**0.0003**	**<0.0001**	0.4004	0.4004	0.8101	0.38
LAR	0.9816	**<0.0001**	0.7235	0.6767	0.4144	0.82
Aerial LAR	0.4273	**<0.0001**	**0.0039**	0.4246	0.6572	0.68

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SRL	0.8996	**0.0033**	0.2011	0.5565	0.1350	0.26

Abbreviations: AG: absolute growth in 2010; AHG: averaged height growth (cm $year^{-1}$), percentage of total tree dry mass devoted to branches (% Branch), stem (% Stem), leaves (% Leaf) and roots (% Root); PT/NPT: ratio of photosynthetic to non-photosynthetic tissues; FRMR: fine root to whole plant mass ratio; Root/Shoot: total root mass to aerial plant mass ratio; Nb. Branches: number of live branches; LMA: leaf mass per area (g m^{-2}); LAR: leaf area ratio (cm^2 g^{-1} plant); Aerial LAR: aerial leaf area ratio (cm^2 g^{-1} aerial biomass); SRL: specific root length (m g^{-1}). Significant effects ($P < 0.05$) are shown in bold.

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FIGURE CAPTIONS

Figure 1. Proportion of the occurrence of YB juveniles found in 2010 across different seedbed types (A); and different microsites (B) in 4 forest stands in southern Quebec managed by selective cutting (SC). For seedbeds: DW: deadwood; MDW: mosses in deadwood; MS: mineral soil; "Other" includes the least frequent seedbed types: mosses and humus. For microsites: PM: pit and mound; S: stump; T: trunk; ST: skid trail; WD: wood debris. Bars show mean ± SE across transects in old (1994-1995) and recent (2004) treatments. Asterisks denote significant differences between old and recent SC stands based on chi-square test results.

Figure 2. (A) Proportion of basal area of main tree species (SC), and (B) proportion of yellow birch (YB) juveniles found on deadwood as a function of species identity of deadwood material for 275 YB juveniles sampled across 4 forest stands in southern Quebec managed by selective cutting. Bars show mean ± SE across transects. ACSA: *Acer saccharum*; BEAL: *Betula alleghaniensis*; *Deciduous* category includes all deciduous species other than ACSA and BEAL, whereas *Conifer* includes all conifer species observed.

Figure 3. Proportion of yellow birch (YB) juveniles found on deadwood seedbed across 4 temperate forest stands in southern Quebec managed by selective cutting (SC) as a function of deadwood decay class and time since harvest (Old (1994-1995) *vs.* Recent (2004)). Categories of decay class are based on Angers *et al.* (2005).

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Figure 4. Effect of tree height and seedbed type on (A) absolute growth of 2010 (AG; cm), and (B) averaged height growth (AHG; total height divided by age; cm/year) for yellow birch (YB) juveniles across 4 forest stands managed by selective cutting (Old, 1994-95 and Recent, 2004). Dots represent predicted values obtained by the ANCOVA models while lines represent corresponding fitted regressions on predicted values (DW, triangles and black line; MDW, circles and dark-grey line; MS, crosses and mid-grey line).

Figure 5. (A) Fine root mass ratio (FRMR; $g.g^{-1}$ plant), and (B) total leaf area on aerial mass (Aerial LAR; $cm^2.g^{-1}$ plant) as a function of seedbed type for 274 yellow birch (YB) juveniles across 4 temperate forest stands in southern Quebec managed by selective cutting (SC). Bars show mean ± SE across stands, and statistically significant differences between seedbed types are denoted with different letters (Tukey–Kramer HSD test, $P < 0.05$).

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Figure 1

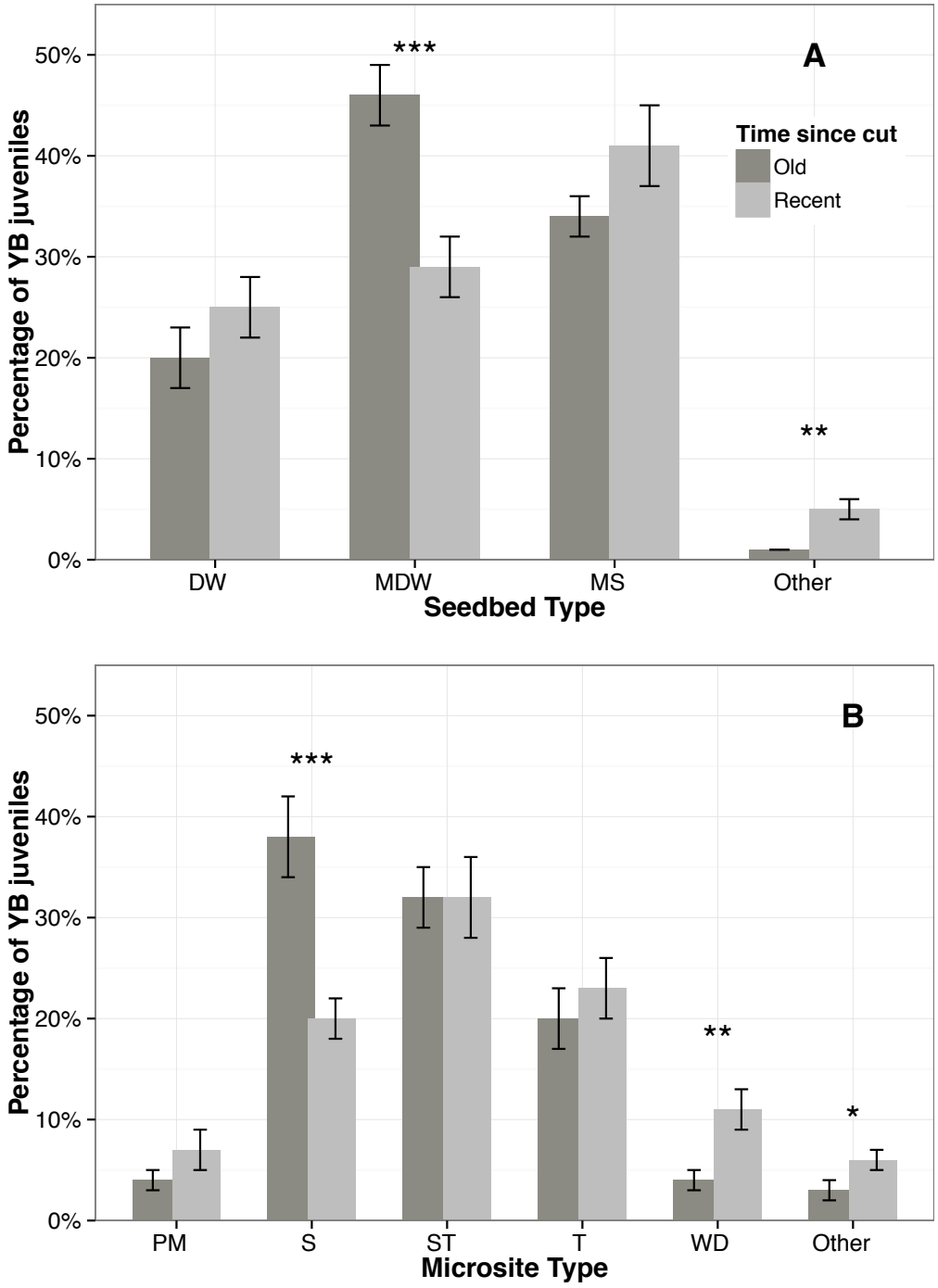

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Figure 2

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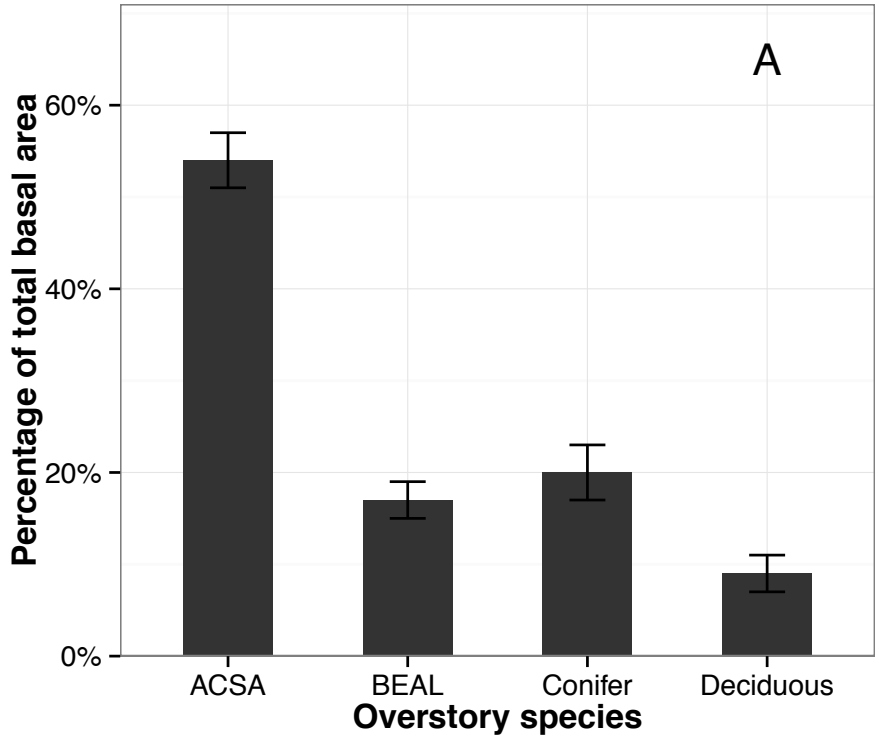

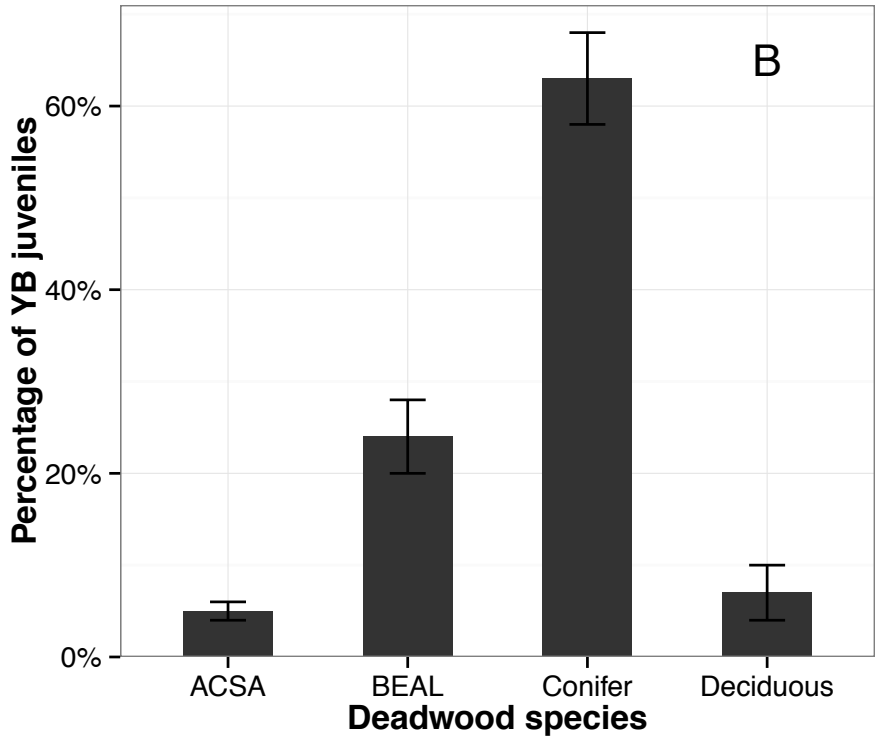

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Figure 3

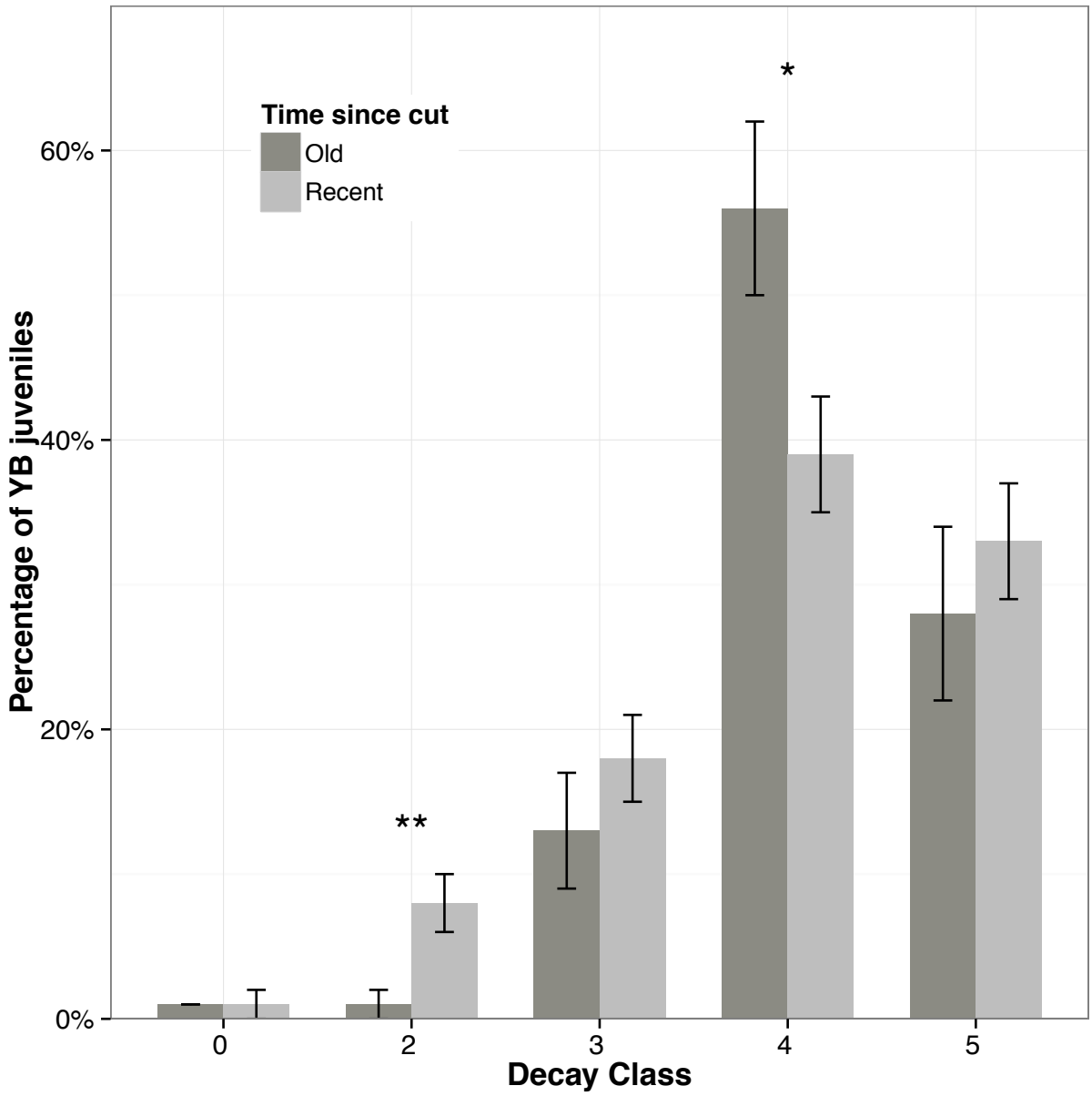

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Figure 4

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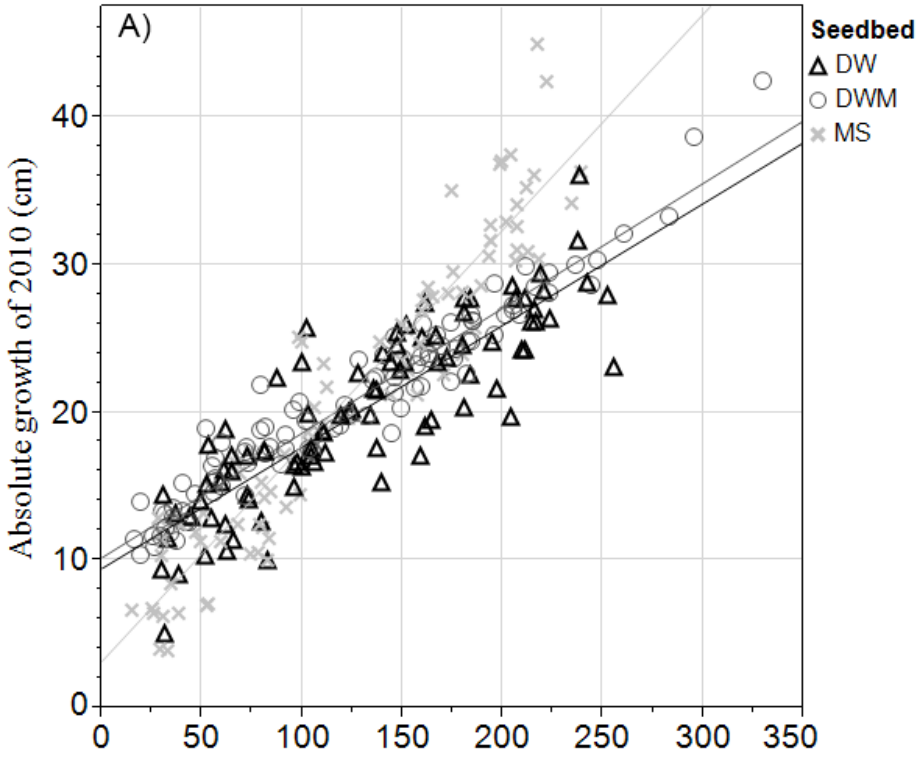

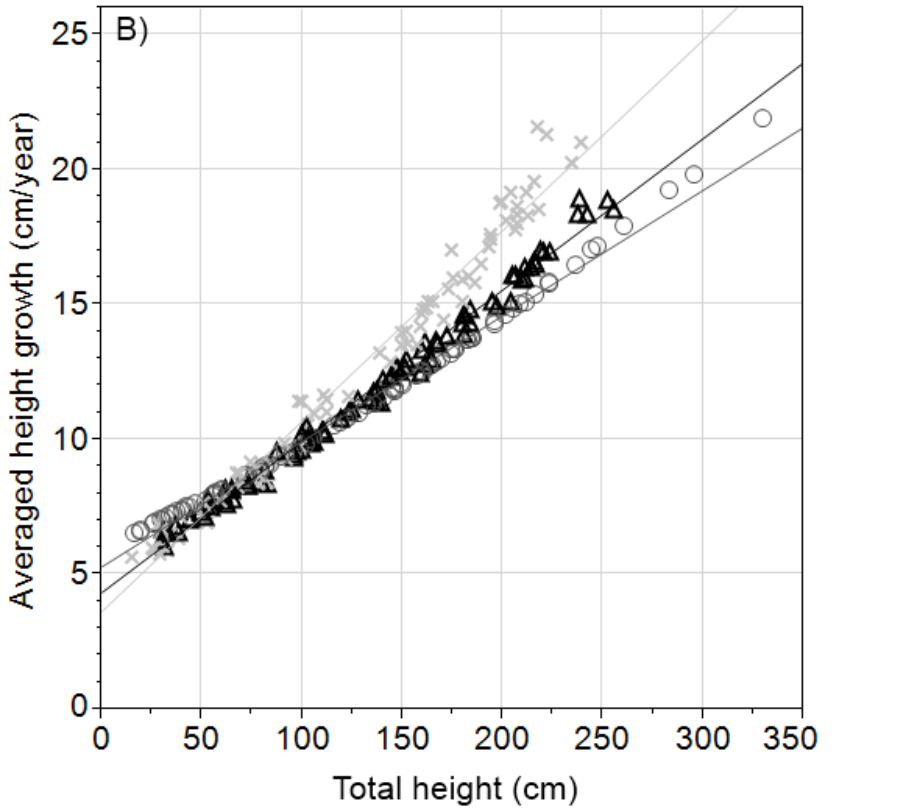

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Figure 5